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# FURTHER FLORISTICS ON LATE TERTIARY LACUSTRINE DEPOSITS IN THE SOUTHERN ARIZONA DESERTS

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Abstract

The unusual edaphic habitats of late Tertiary lacustrine deposits in Sonoran Desert basins of central Arizona have previously been shown to harbor endemic taxa and disjunct taxa from other floristic regions, which inhabited the Sonoran Desert during previous climatic regimes. The infertile limestone soils contrast sharply with the surrounding volcanic soils, excluding the dominant Sonoran Desert vegetation and thereby providing an ecological opening for the disjuncts. The disjunctions provide clues for interpreting the biogeographical history of Arizona. Here, thirteen additional examples are documented. Taxonomic changes to two of the earlier examples, *Eriogonum apachense* and *Hymenoxys acaulis* var. *arizonica*, are discussed. *Erigonum apachense* from the San Carlos Basin is revealed to be a disjunct population of the northern *E. heermannii* var. *argense*, not a separate endemic species; and, a recently named taxon, *Tetraneuris verdiensis*, from the Verde Valley, is shown to be a rayless form of *T. acaulis* var. *arizonica*, not a separate endemic species. The biogeography of *Ericameria nauseosa* var. *juncea* and *Quercus havardii* are considered in more detail. The type locality of *Ericameria nauseosa* var. *juncea* is one of the disjunct localities, not from the main range of the variety. An unusual thicket-forming oak in the Verde Valley is determined to be a disjunct population of *Quercus havardii* from Staked Plains of New Mexico and Texas and the Four Corners of the Colorado Plateau.

Key Words: Arizona deserts, disjuncts, edaphic habitats, endemics, *Ericameria nauseosa* var *juncea*, *Eriogonum apachense*, *Hymenoxys acaulis* var *arizonica*, *Quercus havardii*.

Plant distributions, their geographic ranges, are effected both by current environmental conditions, their ecology, and past environmental conditions, their biogeographical history. In the cases of disjuncts and endemics, biogeographical history can be the most important factor effecting their present day distribution. These species are remnants of previous floras and environmental conditions whose continued existence provides evidence of the regional biogeographical history (Gankin and Major 1964). However, unlike the dominant vegetation adapted to the present environmental conditions, they can only survive in specialized edaphic and climatic microhabitats. These microhabitats allow the relict species to survive in areas of "compensation" that are more favorable to them within an otherwise hostile environment (Cain 1944).

Late Tertiary lacustrine deposits of limy tuffs in basins in the geological Transition Zone across central Arizona (Titley 1984) along the northern edge of the Sonoran Desert within its *Larrea tridentata-Canotia holocantha* Series of the Arizona Upland Subdivision (Brown 1982) provide edaphic refugia for many disjunct and endemic species of various other floristic affinities (Anderson 1996). The infertile limestone soils of the lacustrine deposits present a sharp edaphic contrast with the predominately volcanic derived soils of the Sonoran Desert mountain ranges. The dominant species of the surrounding Sonoran Desert, *Larrea tridentata* (DC.) Coville and *Parkinsonia microphylla* Torr., which are adapted to the zonal volcanic soils are not able to grow on the azonal limestone soils affording an ecological opening for the relict disjunct species to survive. Another factor aiding an ecological opening for relicts is their occurrence at the northern edge of the Sonoran Desert that places the Transition Zone basins both in an ecotonal area where the surrounding vegetation type is not as dominant, and in an area with a comparably more equable climate that is similar to the more mesic paleoclimate in the region (Axelrod 1979; Anderson 1996).

Thus, the microhabitat refugia contain plant communities of biogeographically unusual species combinations not found anywhere else. These refugia consist of disjunct taxa of different floristic origins from north, south and east that normally are far removed in range from each other. In a sense they represent azonal plant communities that occur as an archipelago of atypical vegetative islands within the dominant Sonoran Desert "sea." The documentation of the presence of these relicts as indicators of the past climatic and topographic variability of Arizona and of past floras occupying the current Sonoran Desert provides clues to past floristic patterns and migrations and enhances the knowledge of the biogeographical history of Arizona.

Anderson (1996) documented the only Sonoran Desert occurrences of thirty of these relict taxa in the Transition Zone lacustrine basins

TABLE 1. SPECIES DISTRIBUTIONS AMONG LATE TERTIARY LACUSTRINE DEPOSITS ACROSS CENTRAL ARIZONA. Basins listed left to right from west to east. Species listed alphabetically by genus.

| Species | Anderson mine | Burro creek | Verde valley | San carlos basin | Duncan basin |
|---|---|---|---|---|---|
| *Allium bigelovii* S. Watson | X | X | X | | |
| *Astragalus amphioxys* A. Gray var. *modestus* Barneby | X | X | | | |
| *Cryptantha humilis* (Greene) Payson | | X | | | |
| *Ericameria nauseosus* (Pall. ex Pursh) G. L. Nesom & G. I. Baird var. *junceus* (Greene) H. M. Hall | | X | | | X |
| *Eriogonum heermannii* Durand & Hilg. var. *argense* (M. E. Jones) Munz | | | X | X | |
| *Eriogonum microthecum* Nutt. var. *simpsonii* (Benth) Reveal | | X | X | | |
| *Frasera albomarginata* S. Watson | | | X | | |
| *Houstonia rubra* Cav. | | | X | | |
| *Pediomelum verdiense* S. L. Welsh & M. Licher | | | X | | |
| *Quercus havardii* Rydb. | | | X | | |
| *Stanleya pinnata* (Pursh) Britton | | | X | | |
| *Tetraneuris acaulis* (Pursh) Greene var. *arizonica* K. F. Parker | | | X | | |
| *Townsendia incana* Nutt. | | | X | | |

whose main ranges were from the Chihuahuan, Mohave, and Navajoan (Colorado Plateau) deserts. Following fieldwork in these basins and in two additional lacustrine deposits, the Anderson Mine and the Duncan Basin, thirteen more such examples have been delineated including the newly described Verde Valley endemic, *Pediomelum verdiense* S. L. Welsh & M. Licher, (Welsh and Licher 2010). The taxonomic status of two of the examples considered by Anderson (1996) have been reassessed (Table 1). The lacustrine deposit at the Anderson Mine area (an old 1950's uranium mine site recently test drilled for resumed mining) above the Santa Maria River in Yavapai County at 590 m is part of the mid-Miocene Chapin Wash Formation (Otton 1981). It is approximately 35 km southwest of the Burro Creek deposit at 770 m, and is the furthest west and lowest elevation lacustrine deposit in the Sonoran Desert (Fig. 1). The Duncan Basin containing the Gila Group lacustrine deposit (Nations et al. 1982; Reid and Buffler 2004) is in the Chihuahuan Desert at 1100 m and is the farthest east in Arizona, approximately 5 km from the Arizona/New Mexico stateline.

With two exceptions, *Allium bigelovii* S. Watson and *Houstonia rubra* Cav., all of the additional taxa listed in Table 1 have floristic affinities to the north, primarily to the Colorado Plateau Subprovincial Element (McLaughlin 2007) with extensions into the Great Basin or Mohave Desert. *Astragalus lentiginosus* Douglas var. *wilsonii* (Greene) Barneby (*Anderson 2009-13* ASU) is another northern taxa disjunct in the Verde Valley but not on the lacustrine deposits. Similarly, in Anderson (1996), more of the disjuncts listed (eighteen of thirty) had northern floristic affinities. These southward disjunctions are the result of the more recent southward movement of northern biotic communities, Great Basin Conifer Woodlands and Great Basin Desertscrub (Brown 1982) from the Colorado Plateau into areas of present day Sonoran Desert in Arizona during Pleistocene glacial cycles as documented by pack rat midden studies (Betancourt et al. 1990). The presence of these northern floristic remnants in the Sonoran Desert Provincial Element (McLaughlin 2007) presents another line of evidence, in addition to the pack rat midden studies, for interpreting the biogeographical history of Arizona.

*Allium bigelovii* is now determined to be a northwestward disjunct from the Chihuahuan Desert whose main range is in southwestern New Mexico and southeastern Arizona (Sivinski 2003). The occurrences in the Arizona Sonoran

FIG. 1. Anderson Mine with late Tertiary lacustrine deposit (Chapin Wash Formation), Yavapai County. Note surrounding volcanic mountains.

Desert at the Verde Valley, Burro Creek and the Anderson Mine are disjunct from this main range by as much as 400 km. Previously, the correct floristic status of *Allium bigelovii* in Arizona had been masked by the misidentification of many *Allium* herbarium specimens examined by the author at ARIZ, ASC, and ASU which greatly expanded its apparent geographic range to northern Arizona. *Houstonia rubra* is an eastward disjunct taxon in the Verde Valley from its main range to the southeast in the semi-desert grasslands of southeastern Arizona, eastward to New Mexico, Texas, and Mexico and northeastward in the Colorado Plateau where it extends into pinyon-juniper woodland.

Subsequent systematic research has led to the taxonomic reevaluation of two of the taxa included in Anderson (1996). *Eriogonum apachense* Reveal was listed by Anderson (1996) as an endemic at the San Carlos Basin. At the time of its publication (Reveal 1969), *E. apachense* was described as being closely related to *E. heermannii* Durand & Hilg.; and, its distinction was partially based on its geographic isolation. More recent field work by M. Baker (Southwestern Botanical Research) and R. Denham (private botanist) led to the discovery of *Eriogonum heermannii* var. *argense* (M. E. Jones) Munz on the lacustrine deposits in the Verde Valley; and, the reevaluation of the taxonomic status of *E. apachense* as a possible disjunct population of *E. heermannii* var. *argense*. Later, based on joint field visits to the Verde Valley and San Carlos populations and close examination of their respective *Eriogonum* populations, J. Reveal (Cornell University) and the present author came to the conclusion that the San Carlos *Eriogonum* populations represent disjunct populations of *E. heermannii* var. *argense* and not a different endemic species (Reveal 2005). The biogeographical pattern of these *E. heermannii* var. *argense* populations in the San Carlos Basin follows and further confirms that of the other disjuncts on lacustrine deposits described in Anderson (1996) and helps explain a seeming distributional anomaly.

The locality data of another seemingly out of range collection in southern Arizona of *Eriogonum heermannii* var *argense* (M. E. Jones *s.n.* 1903 RSA!) near Vail, Arizona, had been doubted (Kearney and Peebles [1960] state, "The locality as stated is almost certainly erroneous.") However, another lacustrine deposit, the Oligocene Pantano Formation, outcrops in the Vail area (Brennan 1962; Nations et al. 1982). Its presence could provide potential edaphic habitat for a disjunct population of *E. heermannii* var. *argense* similar to the biogeographical pattern described above and shows that the label locality is not "certainly erroneous." Although it has not been rediscovered during subsequent searches there, a new *Eriogonum* species, *Eriogonum terrenatum* Reveal, was discovered on the Pantano Formation by the present author (Reveal 2004). Its only other occurrences are on another lacustrine deposit, the Pleistocene St. David Formation along the San Pedro River approximately 50 km southeast of Vail (Anderson 2007). Its nearest relatives are *Eriogonum ericifolium* Torr. & A. Gray var. *ericifolium* on lacustrine soils in the Verde Valley and *E. pulchrum* Eastw. farther north on the Colorado Plateau. These related *Eriogonum* species provide another example of the lacustrine biographical disjunct pattern (Anderson 2007).

Anderson (1996) listed *Hymenoxys acaulis* (Pursh) K. F. Parker var. *arizonica* (Greene) K. F. Parker, now treated as *Tetraneuris acaulis* (Pursh) Greene var. *arizonica* (Greene) K. F. Parker (Bierner and Turner 2003, 2006) as a disjunct in the Verde Valley. Later, an endemic to the Verde Valley lacustrine deposits, *Tetraneuris verdiensis* R. A. Denham & B. L. Turner, has been described based on "discoid heads...dwarf habitat, relatively short broad leaves, and long pilose vestiture" (Denham and Turner 1996). The subpopulations described as *T. verdiensis* occur on four small gypsum hills only 10 km to the east of the nearest known population of *T. acaulis* var. *arizonica* (Anderson 1996; Denham and Turner 1996; Godec 2001). A more detailed morphological comparison of these two *Tetraneuris* populations showed that the discoid head is the only consistent morphological difference between them (Godec 2001). Individual discoid plants of *T. acaulis* are known elsewhere within its range (described as *T. eradiata* A. Nelson) but are considered to be conspecific (Bierner and Turner 2003). Although the populations of *T. verdiensis* are entirely discoid, this is a minor morphological difference. *Tetraneuris verdiensis* and *T. acaulis* var. *arizonica* share similar edaphic habitats (Nations et al. 1981), associated species such as the other disjuncts, *Eriogonum ericifolium* var. *ericifolium* and *Salvia dorrii* (Kellogg) Abrams ssp. *mearnsii* (Britton) E. M. McClintock, and close proximity to one another (Godec 2001). Based on these factors, it seems more accurate to consider *T. verdiensis* as a discoid form of *T. acaulis* var. *arizonica*, not as a distinct species (Bierner and Turner 2006).

The type locality of *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird var. *juncea* (Greene) G. L. Nesom & G. I. Baird is a disjunct population in the Chihuahuan Desert on "calcareous bluffs of the Gila River in eastern Arizona very near the New Mexican boundary," (Greene 1881). This locality is far to the south from its normal range of the Colorado Plateau in northern Arizona, southern Utah and adjacent Colorado. A late Tertiary Pliocene lacustrine deposit, the Gila Group, outcrops in this area (Nations et al. 1982; Reid and Buffler 2004) and

FIG. 2. Duncan Basin with late Tertiary lacustrine deposit (Gila Group), Greenlee County. Note lacustrine mudstone in the foreground and volcanic mountains on the horizon.

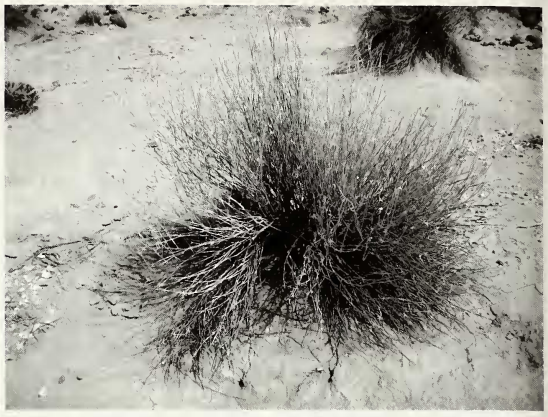

FIG. 3. *Ericameria nauseosa* var. *juncea* on lacustrine mudstone of the Gila Group, Duncan Basin, Greenlee County.

may be the "calcareous bluffs" habitat mentioned on Greene's label (Fig. 2). The author collected *E. nauseosa* var *juncea* (Fig. 3) on lacustrine badlands of the Gila Group (*Anderson 2009-10* ASU) in the same vicinity as L. Anderson whose collection label (*L. Anderson 4757* 4 Oct 1978 RSA!) states "probable type locality." The variety is also present at the Burro Creek lacustrine site. In addition, another Colorado Plateau/Great Basin disjunct, *Atriplex confertifolia* (Torr. & Frem.) S. Watson, occurs with the *Ericameria* in the Duncan Basin (*Anderson 2009-09* ASU). It is also present in the San Carlos Basin (Anderson 1996).

A peculiar thicket-forming, deciduous oak was discovered by the present author and N. D. Atwood (Brigham Young University) on lacustrine soils of the Verde Formation in the Verde Valley (*Anderson and Atwood 93-13* ASU). L. Landrum (Arizona State University) made a population series of collections (*Landrum 8241-8256, 8258, 8261, and 8263a* ASU) in 1994 and determined it to be *Quercus havardii* Rydb (Fig. 4). Typical *Q. havardii* is a species from the Staked Plains of the Texas panhandle and adjacent New Mexico that occurs in areas of shifting sands in which its thickets form small sand dunes. Other populations attributed to *Q. havardii* also occur in the Four Corners region of southeastern Utah and northeastern Arizona (Tucker 1970; Nixon 1997). Tucker (1970) has interpreted them as ancestral *Q. havardii* populations introgressed by *Q. gambelii* Nutt., not pure *Q. havardii* although he states that the populations are "moderately homogeneous" and not a hybrid swarm. The sandy habitat of *Q. havardii* in the Four Corners is similar to that of the Stake Plains. The anomalous occurrence of the typically sandy habitat dwelling *Q. havardii* on lacustrine limestone in the Verde Valley is an example of substrate switching whereby a disjunct population occurs on a different, even opposite, edaphic habitat from that of its normal range that provides an azonal edaphic refugia (Anderson 1996).

FIG. 4. *Quercus havardii* thicket on Verde Formation limestone, Verde Valley, Yavapai County. Note lacustrine edaphic habitat in foreground and *Canotia holacantha* Torr. in background.

Based on his research that "the species is more or less stable and tends to be habitat specific," Welsh (2003) has recognized the Four Corners populations as a separate species, *Quercus welshii* R. A. Denham ex Welsh. The Verde Valley population appears morphologically similar to the Four Corners populations and could thus be treated as a disjunct population of *Q. welshii*.

As a more southwestern population location, the discovery of *Quercus havardii* in the Verde Valley gives credence to Tucker's postulation that the present day disjunct distribution pattern of *Q. havardii* between Texas/New Mexico and Utah/Arizona is due to its migration northward along both sides of the Rocky Mountains in New Mexico with the glacial retreat from a previously

more continuous ancestral distribution to the south and west of its present distribution (Tucker 1970). The documentation of *Q. havardii* in the Verde Valley is another important instance of the use of species distributions to elucidate past biogeographical patterns.

The biogeogaphical documentation of the many disjuncts in the Verde Valley (Table 1) demonstrates its importance for botanical conservation. Based on the large number of special status plant species occurrences and its rapid population growth, the Verde Valley has a high priority need for botanical conservation. A portion of the Verde Valley lacustrine deposits around the occurrences of the federally endangered *Purshia subintegra* (Kearney) Henrickson and other of the rare Verde Valley plants mentioned above has been designated the Verde Valley Botanical Area by the U.S. Forest Service.

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## Appendix 1

## Specimen Citations for Disjuncts and Endemics

Specimen citations are listed by taxonomic family and basin location within family: Anderson Mine (AM), Burro Creek (BC), Verde Valley (VV), San Carlos Basin (SC), and Duncan Basin (DB). Herbarium labels contain more specific habitat and locality data (see SEINet for electronic database of Arizona herbaria including species descriptions, pictures, label data, and distribution map; data for rare species may be masked and permission from herbaria curators is required for access). All cited specimens are deposited at ASU unless otherwise indicated or duplicates of ASU specimens are present at other Arizona herbaria.

### ALLIACEAE

*Allium bigelovii* S. Watson – AM: 20 Apr 1980, *Butterwick and Hillyard 6165*; 7 Apr 2008, *Anderson 2008-03*. BC: 20 Apr 1938, *Crooks & Darrow s.n.* (ARIZ); 18 Apr 1941, *Darrow & Benson 10906* (ARIZ); 10 Apr 1980, *Butterwick and Hillyard 4504*; 24 Apr 2008, *Anderson 2008-07*. VV: 22 Apr 1978, *Wetherill s.n.* (MNA); 30 Apr 1978 *Haskell & Deaver 2149* (MNA); 22 Apr 1978, *Lambrechtse 30* (ASC); 16 Apr 1988, *Morefield and Windham 1324* (ASC).

### ASTERACEAE

*Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. I. Baird var. *juncea* (Greene) H. M. Hall – BC: 17 Sept 1935, *Peebles 12587* (ARIZ); 31 Oct 1978, *Butterwick 4137*; 27 Sept 2008, *Anderson 2008-22*. DB: 5 Sept 1880, *E. L. Greene s.n.* (NDG); 4 Oct 1978, *L. C. Anderson 4757* (RSA); 30 Apr 2009, *J. L. Anderson 2009-10*.

*Tetraneuris acaulis* (Pursh) Greene var. *arizonica* (Greene) K. F. Parker – VV: 22 Apr 1987, *Boucher 770* (ASC); 8 June 1995, *Anderson 95-17*; 2 Feb 1999, *Anderson with Godec 99-1*; 26 May 1999, *Anderson with Godec 99-15*; 17 Nov 1999, *Baker 13675*; 14 May 1995, *Denham, Forbes, and Searle 1835, 1836, 1837, 1838, 1839* (all paratypes of *Tetraneuris verdiensis*) and 1840 (holotype of *Tetraneuris verdiensis*) (TEX).

*Townsendia incana* Nutt. – VV: 15 Apr 1978, *Lehto 22583*; 24 June 1979; *Ertter and Strachen 2941*; 7 May 1995, *Anderson 89-39*; 28 May 1993, *Rebman 1865*; 1 May 1999, *Anderson 99-10*.

### BORGINACEAE

*Cryptantha humilis* (Greene) Payson – BC: 20 Apr 1938, *Crooks & Darrow s.n.* (ARIZ); 18 Apr 1941, *Darrow & Benson 10905* (ARIZ); 10 Apr 1947, *Gould & Darrow 4248* (ARIZ); 11 Apr 1976, *Fugate & McLaughlin 1090* (ARIZ); 10 Apr 1979, *Butterwick/ Hillyard 4502*; 6 Apr 1987, *Anderson 86-7*; 27 Apr 2000, *Anderson 2000-4*; 8 Apr 2004, *Anderson 2004-5*.

### BRASSICACEAE

*Stanleya pinnata* (Pursh) Britton – VV: 1 June 1970, *Harris s.n.*; 26 May 1999, *Anderson 99-17*.)

### FABACEAE

*Astragalus amphioxys* A. Gray var. *modestus* Barneby – AM: 20 Apr 1980, *Hillyard 6166, 6170*; 10 May 1995, *Anderson 95-12*. BC: 18 Apr 41, *Benson 10904* (ARIZ); 10 Apr 1979, *Hillyard 4491*; 9 May 1995, *Anderson 95-11*.

*Pediomelum verdiense* S. L. Welsh & M. Licher – VV: 9 Jun 1941, *Chas. F. Harbison 41.312* (ARIZ); 7 May 1961, *D. Demaree 43936* (ARIZ); 7 May 1989, *Anderson 89-43*; 23 Apr 1992, *Wojciechowski & Sanderson 212* (ARIZ); 30 May 1998, *Hodgson 10397*; 25 Apr 2003, *Rink & Murov 1840* (ASC); 18 Apr 2003 *M. Licher 1911* (BRY holotype, ASC isotype).

### FAGACEAE

*Quercus havardii* Rydb. – VV: 10 June 1993, *Anderson and Atwood 93-13*; 22 June 1994, *Landrum et al 8241-8256, 8258, 8261, 8263a*; *Anderson 2009-47, 48, 49*.

### GENTIANACEAE

*Frasera albomarginata* S. Watson – VV: 2 May 1964, *Eaton 47*; 18 May 1984, *Ricketson 1227*; 26 May 1999, *Anderson 99-16*.

### POLYGONACEAE

*Eriogonum heermannii* Durand & Hilg. var. *argense* (M. E. Jones) Munz – VV: 23 Oct 1995, *Baker 12078*; 10 Oct 2003, *Baker 15652*; 17 Oct 2003, *Reveal 8412, 8413*. SC: 7 Sept 1968, *Pinkava, Keil, & Lehto 13400* (isotype of *Erigonum apachense*); 4 Oct 1967, *Keil, Pinkava, & Lehto 10134*, 8 May 1968, *13018* (both paratypes); 21 Oct 2003, *Reveal 8418, 8419*.

*Eriogonum microthecum* Nutt. var. *simpsonii* (Benth) Reveal – BC: 17 Sept 1935, *Kearney 12588* (ARIZ); 31 Oct 1978, *Butterwick 4135*; 5 Nov 1983, *Parfitt 3160*; 27 Sept 2008, *Anderson 2008-23*. VV: 19 Sept 1976 *Lehto 20696*, 20718; 29 May 1981, *Van Devender s.n.* (ARIZ); 20 Sept 1984, *Schaack 1326* (ASC); 8 Sept 1988, *Ruffner s.n.* (ASC); 20 Sept 1992, *Baker 10245*; 23 June 1993, *Rowlands s.n.* (ASC); 22 Oct 1994, *Fishbein 2004* (ARIZ); 1 July 1995, *Wright 1597*; 20 Aug 1995, *Baker 11919*; 17 Oct 2003, *Reveal 8414*.

### RUBIACEAE

*Houstonia rubra* Cav. – VV: 2 May 1969, *Pinkava 4960*; 12 Feb 1999, *Anderson 99-2*; 1 May 1999, *Anderson 99-11*.